INVESTIGATIONS ON THE PHYLOGENY OF THE ANGIOSPERMS

NO. 2. ANATOMICAL EVIDENCES OF REDUCTION IN CERTAIN OF THE AMENTIFERAE

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(WITH PLATES III–V AND THREE FIGURES)

The earlier taxonomists by systematic studies, principally of external characters, have contributed much toward a truly natural classification of the angiosperms, but the problem is such an intricate one that in searching for a satisfactory solution evidence from all fields of botanical research must be considered and harmonized.

In view of the assistance given by comparative anatomists in elucidating the phylogeny of gymnosperms and lower vascular plants, the recent hypothesis of Professor JEFFREY and his pupils, in regard to the development of "aggregate," "compound," and "multiseriate" rays in dicotyledonous angiosperms, merits careful consideration by taxonomists, since, if shown to rest on secure foundations, it is likely to produce radical changes in existing systems of classification.

The "aggregate" ray hypothesis

The salient features of this hypothesis may be summarized as follows: The angiosperms have not been derived from the Bennettitales, but from ancestors which possessed only linear or uniseriate rays, such as are a well developed feature of the Coniferales. During the warmer times of the Mesozoic, sheets of parenchymatous tissue were "built up" from congeries of uniseriate rays about the traces of leaves which persisted for a number of seasons. The influence at work in the development of this tissue was originally the demand for the storage of assimilates descending from the large leaves of these earlier angiosperms. These "foliar" rays have persisted in their very primitive "aggregate" condition (composed of congeries of small rays), and in their more advanced "compound" condition (completely parenchymatous), in primitive families of the dicotyledons. With the advent of a severe winter season and the consequent acquirement of the deciduous habit in connection with the leaves, the organization of these storage systems about the leaf traces as permanent centers was no longer advantageous or desirable. Thus in the development of the "multiseriate" type of ray which characterizes the majority of living dicotyledons, the enlarged units of the aggregating mass of foliar ray tissue have been diffused more or less uniformly throughout the stem. Besides being less unwieldy, this system of smaller rays affords equally large capacity for storage and a more convenient general relation between conducting, supporting, and storage tissue.

The principal arguments in favor of this hypothesis were first formulated in a paper presented by JEFFREY ('09) before the Botanical Society of America at Baltimore.

> One of the most striking triumphs of modern plant anatomy is to have discovered many examples of recapitulationary confirmation of the principle of evolution. To take a modern and striking example, let us consider our common and flourishing northern genus, the oak. You are all familiar with the very broad rays which constitute so ornamental a feature of the structure of oak wood. You are likewise doubtless aware that the weight of paleobotanical evidence speaks for the derivation of the oaks from ancestors resembling the chestnuts, since the older oaks approach the chestnuts both in their foliage and in their reproductive organs. The wood of the chestnut differs, however, strikingly from that of oaks by the entire absence of large rays. It has been recently discovered that certain oaks of the gold gravels (Miocene-Tertiary) of California have their large rays composed of aggregations of smaller rays. In the seedlings of certain of our existing American oaks this condition, interestingly enough, is a passing phase, which by the loss of the separating fibers in the congeries of small rays produces the characteristic large rays of the adult. This condition of development in the living oaks is all the more significant because in certain breech-fertilized or chalazogamic amentiferous trees of the present epoch, such as the alder, the hazel, and the hornbeam, such aggregated, so-called false, rays are a permanent feature of structure in the adult. From the anatomical side, in the case of the lower Amentiferae, we have accordingly at the same time an interesting example of the general law of recapitulation and a confirmation of the view expressed by TREUB and NAWASCHIN, on evidence from the gametophytic and reproductive side, that the breech-fertilized Amentiferae are relatively primitive angiosperms.

The arguments blocked out in this paper have been elaborated under JEFFREY's direction by several students (see bibliography).

Especially significant are two collateral lines of evidence which have played an important part in amplifying the original hypothesis. The first of these is concerned with the connection between certain "aggregate" and "compound" rays and the traces of leaves, a phenomenon which is said to indicate conclusively that "aggregate" and "compound" rays were "built up" for purposes of storing the assimilates descending from the large persistent leaves of mesozoic angiosperms. The second line of evidence deals with the apparent disintegration of "foliar" rays in passing from the first formed to the mature portions of the stems of certain Ericales, Fagales, and Casuarinaceae. This ontogenetic sequence has been interpreted as indicating that the "multiseriate" type of ray originated from the diffused portions of "aggregate" or "compound" rays.

Objections to the "aggregate" ray hypothesis

In endeavoring to trace certain steps of the evolutionary history of the so-called "aggregate" and "compound" rays in the Fagales, one of the writers (BAILEY '11) discovered indications of reduction in *Castanea* and *Alnus*. Additional investigations ('12) of these genera, and of *Castanopsis*, *Ostrya*, and *Carpinus* revealed much evidence for believing that the "aggregate" and "compound" rays have disappeared or are in the process of disappearing from living species of these genera. Furthermore, GROOM ('11) has suggested that the small rays of *Quercus* may have originated by the disintegration of primitive wide multiseriate rays. It is somewhat difficult to harmonize completely these observations with the general trend of the investigations upon "wide" rays, since they introduce the possibility that the congeries of small rays (the so-called "aggregate" rays) may be in every case stages in the "breaking down" rather than in the "building up" of wide rays. This fact is particularly significant when we consider that the "aggregate" ray hypothesis derives much of its support from the theory that the chalazogamic Amentiferae are in all probability the most primitive living angiosperms, for many botanists, from comparative studies of sporophytes and gametophytes, consider that these angiosperms with unisexual flowers are reduced rather than truly primitive.

The phenomenon of chalazogamy, which was considered at first of great phylogenetic value, cannot, in view of later investigations, be considered a reliable criterion for the determination of the position of plants in a phylogenetic sequence. The paleontological evidence which has been cited cannot be considered to be entirely convincing, since "multiseriate" rays are found in middle and upper cretaceous dicotyledons, although according to the "aggregate" ray hypothesis they are the most recent development of the angiosperm ray. If "aggregate" and "compound" rays originated for purposes of storing the assimilates descending from the persistent leaves of mesozoic angiosperms, and were later replaced by "multiseriate" rays as an adaptation to the advent of a severe winter season and the consequent acquirement of the deciduous habit by the leaves, we should hardly expect to find the "multiseriate" ray well developed in cretaceous angiosperms or in families which have lived in moist, warm, tropical conditions since ancient times. It is a notable fact, therefore, that "multiseriate" rays are characteristic of such typically tropical families as the Lauraceae, Anonaceae, Ebenaceae, Rubiaceae, Myristicaceae, Apocynaceae, Myrtaceae, etc., although there is no evidence to show that these families have been exposed to a refrigerated climate since the Mesozoic. On the other hand, the "aggregate" ray, which is comparatively infrequent, characterizes the obviously reduced xerophytic Casuarinaceae and the temperate families Betulaceae, Fagaceae, and Ericaceae. Apparently, therefore, the most conclusive evidence that has been advanced in favor of the origin of the "aggregate" and, *pari passu*, of the "compound" and "multiseriate" rays must be considered to be that derived from the study of the phenomena of recapitulation.

STRUCTURE OF SEEDLINGS

We have noted above that JEFFREY places much emphasis upon the fact that the first formed rays of seedling oaks are all of the uniseriate type that occur throughout the wood of the supposedly very primitive chestnut. In white oaks with deciduous foliage (subgenus *Lepidobalanus*) this primitive condition persists until the plants have attained considerable size. These oaks, therefore, are assumed to be more primitive than oaks of the subgenus *Erythrobalanus*, since in the latter the "aggregation" and "fusion" of rays begins much earlier. Similarly, the "live" or "evergreen" oaks are regarded as more primitive than either of these types, since they possess even in the mature wood "aggregate" tissue from which the separating fibers have not been entirely eliminated.

The writers have recently examined seedlings of different species of the Fagales, and have found phenomena that are apparently of considerable interest. Especially significant are the effects of different degrees of vigor upon the development of ray structures in seedling plants. Suppressed, slow-growing, feeble plants are characterized in many cases by the retarded development of large rays. In fact, the effect of stunted growth may be so strongly marked that only uniseriate rays are formed in stems 30–50 years old. On the other hand, in plants with large, vigorous, well nourished growing points the development of large rays is often accelerated. Vigorous specimens of certain oaks, e.g., *Quercus rubra* L., may even possess wide rays (so-called compound or completely parenchymatous rays) in the first formed portion of the seedling stem (figs. 3 and 13). In the ontogeny of these rays, as in those of *Fagus grandifolia* Ehrh. and *F. sylvatica* L. (fig. 1), there are no putative stages of "aggregation" and fusion.

It is somewhat difficult to explain satisfactorily the facts of seedling anatomy in the Fagaceae, since a strict application of the doctrine of recapitulation might be considered to indicate in the case of certain seedlings that the multiseriate type of ray is primitive, whereas in other young plants it seems to show that wide rays have been "built up" phylogenetically from congeries of uniseriate rays.

The seedling or young plant has been shown in a number of cases to retain characters that are in all probability ancestral, but these phenomena have been interpreted differently by different investigators. HILL and DEFRAINE and others maintain that the seedling is very sensitive to changes in its internal or external environment and therefore of little or no value for phylogenetic purposes. Primitive structures persist only where they are of functional importance in the young plant. In opposition to this are the views of JEFFREY, who considers that HAECKEL'S doctrine of recapitulation is of "universal validity," as invariably operative as the laws of chemistry, physics, and the other cognate sciences. A more conservative working hypothesis which combines elements from each of these antagonistic extremes is held by other biologists, who believe that there are categories of predominantly conservative and of predominantly variable characters, just as there are organs or regions of the plant that are more retentive of primitive characters than others. The mere fact that certain ontogenetic characters have been found to be extremely inconstant and sensitive to physiological conditions does not necessarily invalidate the doctrine of recapitulation. Nor does the fact that the young plant has been shown in certain cases to retain ancestral features indicate that every seedling character is of phylogenetic value. The seedling may display a strong tendency toward conservatism and still be subject to environmental influences, just as the behavior of a falling body may be influenced by other forces than that of gravity. However, the fact that any character in the young plant may be subject to modification by physiological changes makes it difficult in many cases to distinguish palingenetic from cenogenetic features. Phylogenetic conclusions drawn from the study of the structure of seedlings are not conclusive unless substantiated by reliable corroborative evidence.

In view of the somewhat paradoxical behavior of wide rays in the seedling stem, the structure of other regions which are supposed to be conservative and retentive of ancestral characters has an important bearing on the problem under discussion.

THE ROOT

In a recent paper JEFFREY ('12) makes these comments upon the conservatism of the root:

> There are organs of the plant, for example, even more strongly retentive of ancestral characters than the seedling stem. Perhaps the most conservative organ is the root, which varies so little in its fundamental organization throughout the vascular plants that one formula will represent the organization of all roots.

The roots of *Fagus grandifolia* and *F. sylvatica* (fig. 2) possess even in the first formed secondary xylem multiseriate rays which radiate from the clusters of protoxylem. These wide sheets of homogeneous ray parenchyma do not arise by a process of "compounding." Similarly, the "secondary" multiseriate rays which develop as the root increases in circumference are not formed by the "aggregation" and "fusion" of small rays, but originate, as they do in the young stem and mature shoots, by the widening of a single uniseriate ray. Conditions equally significant exist in other genera of the Fagales. For example, wide multiseriate rays occur in the first formed portions of the roots of *Quercus velutina* Lam., although in the seedling stem only uniseriate rays are formed by the first activity of the cambium. On the other hand, certain species of the Betulaceae and Fagaceae possess only uniseriate rays in the first formed portions of the roots, although so-called "aggregate" or "compound" rays may develop during subsequent growth (fig. 6). In the root, as in the seedling stem, variations in vigor and other physiological conditions produce marked variations in the development of rays. Vigor usually accelerates the formation of large rays and feeble or stunted growth tends to reduce their size or retard their development.

THE REPRODUCTIVE AXIS

Scott in his studies of cycads was the first to point out in a convincing manner the importance of the anatomy of the reproductive axis as a possible seat of conservatism. More recently Jeffrey, working upon the comparative anatomy of gymnosperms, has reached the conclusion that this region is even more retentive of ancestral characters than is the seedling stem.

The flowering axes of many dicotyledonous plants are less favorable for the study of structures which occur in the secondary wood than are the cone axes of gymnosperms, since they often are herbaceous or possess only a narrow zone of secondary tissue. It is fortunate, therefore, that the peduncles of many species of *Quercus* and *Casuarina* have wide zones of secondary wood and well developed rays. The peduncles of the red or black oaks (subgenus *Erythrobalanus*) are particularly interesting, since they persist through two growing seasons and possess in consequence two layers of secondary tissue. The development of ray structures in these species is well illustrated by the peduncles of *Quercus coccinea* Moench. and *Q. ilicifolia* Wang. Multiseriate rays are formed by the first activity of the cambium and show no putative stages of "aggregation" and "fusion" in their ontogenetic development (fig. 15). Conditions equally significant have been observed by the writers in the peduncles of *Casuarina suberosa* Otto and Dietr., a species which possesses well developed "aggregate" rays in the seedling stem (fig. 7). The peduncles of *Quercus pedunculata* Ehrh., *Alnus maritima* (Marsh) Muhl., *A. incana* L. Moench., and *A. yasha* Matsum, are slender and possess narrower zones of secondary tissue. However, even in these peduncles biseriate and triseriate as well as uniseriate rays are often formed by the first activity of the cambium.

THE NODE

SCOTT, JEFFREY, and others have emphasized the conservatism of the leaf trace and neighboring tissues. The structure of the nodal region is therefore important in a discussion of the origin and development of "aggregate" and "compound" rays.

Throughout the Fagales there is a marked tendency for large rays to be more strongly developed in the young shoot in the vicinity of those strands of the vascular cylinder which are about to pass out to the leaves. These rays are in many cases composed of homogeneous ray parenchyma, whereas the wide rays in other radii of the stem arise apparently by a "compounding" process from congeries of uniseriate rays. Perhaps the most significant conditions are those which occur in supposedly primitive representatives of the Fagales. Among the Betulaceae, for example, vestiges of "aggregate" rays may occur in the nodal region when the internodes possess only uniseriate rays (fig. 12). Similar conditions are of frequent occurrence in the white oaks (subgenus *Lepidobalanus*). Stems of *Quercus alba* L. often possess for many years only uniseriate rays except in the vicinity of the lateral traces of the leaves (fig. 10). The root may likewise be devoid of wide sheets of ray tissue except in the vicinity of the vascular elements which pass out to the rootlets (figs. 6, 11, and 20). In this region vestiges of wide sheets of homogeneous ray parenchyma occur. Especially significant are the wide multiseriate rays which radiate from the clusters of primary elements in the hypocotyledonary region of young plants of *Quercus virginiana* Mill., a "live" or "evergreen" oak which often possesses "aggregate" rays in the mature wood of the stem.

THE FIRST ANNUAL RING

The first elements formed by the cambium or lateral growing point (the so-called first annual ring) have been considered by JEFFREY, THOMSON, and others to be conservative of ancestral characters. It has been shown in the preceding pages that the first formed portions of the seedling stem and root may possess often only uniseriate rays which later appear to "aggregate" and form wide sheets of ray tissue (figs. 4 and 6). However, in certain cases the first annual ring of vigorous shoots and roots may possess "aggregate" and "multiseriate" rays when the mature portions of these organs develop only uniseriate rays. For example, vestiges of wide multiseriate rays have been observed in very vigorous young roots of *Castanea dentata* (Marsh) Borkh. (figs. 11 and 20). These rays occurred in the vicinity of the vascular strands which supply the rootlets. Similarly, vestiges of "aggregate" rays occur in the first formed portions of vigorous shoots and roots of *Alnus mollis* Fernald, *Alnus acuminata* H.B.K., and *Ostrya virginiana* (Mill.) Koch, species which do not possess "aggregate" or "compound" rays in the normal mature wood.

The structure of vigorous mature shoots of *Quercus velutina* and *Q. rubra* is also significant. As is well known, the primary vascular bundles of the oak are not grouped about a more or less cylindrical pith (except in the peduncle and epicotyledonary region), but about one that is deeply fluted (figs. 9 and 10). In cross-section the young twigs possess, therefore, a cambium layer that is composed of ten alternating convex and concave arcs. Thus five large wedge-shaped segments of secondary xylem are formed, which include between them five narrow depressed segments with more nearly parallel sides. This condition may persist in some cases for a number of years, but usually is replaced sooner or later by a stem of cylindrical outline. Vigorous shoots of the red and black oak (fig. 19) resemble the normal stem of *Fagus grandifolia*, since the gaps which separate the numerous distinct clusters of protoxylem subtend an equal number of multiseriate rays. There is this difference, however, that in subsequent growth of the twigs not all of these so-called primary rays increase in breadth as do those of the vigorous seedling stem (fig. 3), peduncle (fig. 8), and beech (fig. 1). The multiseriate rays which occur in the first annual ring of the narrow depressed segments gradually decrease in width during the next two years' growth and become uniseriate.

The structure and development of rays in the first annual ring of mature shoots are subject, as in the seedling stem, the root, and the peduncle, to marked variations under different physiological conditions. Thus wide rays show a strong tendency to become more numerous and parenchymatous in vigorous, well nourished shoots than in feeble, stunted, or suppressed twigs.

TRAUMATIC REGIONS

JACKSON called attention to numerous cases of reversion to supposedly ancestral types of structure under abnormal growth conditions or as a result of traumatism. JEFFREY, working largely with the internal structure of the gymnosperms, has emphasized the importance of traumatic reactions in the study of phylogeny. His contribution upon recapitulations in those regions of the plant which are assumed to be conservative, such as the root and seedling, is particularly significant, since injuries in these regions are said to recall ancestral characters when reversions cannot be induced traumatically in the mature stem.

The wound reactions of the Fagales are accordingly of interest in a consideration of the "aggregate" ray hypothesis. It has been found by the writers that the stimulating and irritating effect of certain types of injuries (whether mechanical or pathological) often accelerates the development of wide rays. The results of very severe injuries which have a marked distorting effect upon the tissues subsequently formed by the cambium are in some cases very different from these. Such injuries retard the development of large rays, just as feeble or stunted growth has been shown to retard the development of wide rays in seedlings and roots.

The stimulus of certain injuries may produce "aggregate" or multiseriate rays in plants or portions of plants which normally do not possess these structures. For example, when infected with the chestnut bark disease, *Endothia parasitica* Murrill, the chestnut may form large, completely parenchymatous sheets of ray tissue (fig. 16), just as "aggregate" or false rays may be recalled in the stems and roots of Betulaceae which normally possess only uniseriate rays (fig. 12). Wide multiseriate rays may also be induced in certain of the Betulaceae by traumatic stimuli. Especially significant are the effects of injuries in seedlings, roots, and the first formed portions of the mature shoots. Injured seedlings of *Quercus velutina* show an abrupt transition from congeries of uniseriate rays to wide sheets of homogeneous ray parenchyma. Furthermore, a seedling stem or root of *Quercus alba*, which possesses only uniseriate rays, will, when injured, form wide multiseriate rays (fig. 21). These rays often develop without indication of the putative stages of "compounding" (fig. 6). Similar phenomena occur in the first formed portion of mature shoots, in those radii of the stem which do not normally possess wide rays (fig. 10).

Discussion of evidence from conservative regions

In applying HAECKEL'S doctrine of recapitulation, the fact that plants develop by the activity of growing points or meristems rather than by interstitial growth has not always received sufficient consideration. Among higher animals the embryonic and very plastic stages of development are replaced by more highly organized and stereotyped conditions during early stages of ontogeny. In plants, however, the undifferentiated meristematic tissues retain much of their primitive plasticity throughout the life of the individual. This is shown by the fact that the growing points or meristems of mature plants are potentially able to reproduce the whole organism. Owing to this fact, that embryonic types of tissue are active throughout the life history of plants, phenomena of recapitulation need not be confined necessarily to the so-called seedling plant, and may be expected to be more varied than in the higher animals. Thus, there appears to be no fundamental a priori objection to the supposed natural conservatism of the first annual ring, root, node, reproductive axis, or any other particular region. However, the meristematic tissues of the developing plant are in all probability more subject to modifying environmental influences than are the embryos of the higher animals. It is therefore not at all surprising that in many cases the normal conservatism of the embryonic tissues in any region should be more or less neutralized by local physiological changes in the same way that reversions to a more primitive type of structure may be recalled by abnormal stimuli or by traumatism. Nor is it necessary to suppose that all regions of the plant will be subject simultaneously to similar modifying influences. In any given individual or group of individuals, palingenetic characters may occur in one or more regions when they have been lost or replaced by cenogenetic structures in others. It may be seen, therefore, that very misleading conclusions will undoubtedly be drawn by assuming that a given character which appears in a certain conservative region of the plant is primitive, unless reliable corroborative evidence exists. In determining the possible antiquity of a given character it is essential that its structure, development, and behavior under different environmental and physiological conditions should be studied and compared throughout each representative of a wide range of living and, if possible, of fossil forms.

The results of such investigations are in general most conclusive when concerned with categories of characters which have been termed "degradational" or "regressive," that is, characters which are being reduced or lost. JACKSON ('99), in his study of the leaves of a number of gymnosperms and angiosperms, has contributed much toward the elucidation of the behavior of these characters. He has shown that in plants which are losing foliar characters by reduction or simplification the ancestral structures are recalled on vigorous, well nourished stems, or in tissue subject to stimulating types of injury. On the other hand, stunted, feeble, senile conditions tend to hasten the process of reduction, just as on stunted or sickly mature twigs or very old specimens, of a species which has not suffered reduction; the leaves may undergo an incomplete development and revert to the seedling type through a failure in their individual ontogeny to develop full specific characters. The suppression of characters may progress in two ways. In most cases, the young plant, although more conservative in acquiring new foliar characters, is more retentive of these characters, once they become firmly fixed, than are most regions of the mature stem. On the other hand, marked changes in the environment or physiological activity of the young plant may more or less neutralize the effects of its natural conservatism. Under such conditions the seedling may develop cenogenetic characters or lose structures which are retained in mature portions of the plant. Thus JACKSON and COPE have shown that animals and plants may lose ancestral characters by "retardation of development. That is, features may appear at later and later stages in development until they finally disappear."

Internal structures appear in general to behave in regression and progression much as do external foliar characters. That vigorous or stimulated types of growth tend to recall characters which have been reduced has been illustrated, for example, by the recurrence in such types of tissue of marginal tracheids in the Cupresseae, of resin canals in the Taxodieae, and of wood parenchyma in the later Araucarieae. It also seems to be true that the influence of vigor and stimulating injuries in recalling reduced characters are most effective in regions which are supposed to be conservative, such as the first annual ring, root, node, and reproductive axis.

In the Fagales there is apparently a very complete series of species in which the successive stages of the reduction of wide multiseriate rays can be traced in detail. This process of reduction has taken place in most species by "retardation of development," accompanied by a greater or less degree of disintegration of the wide sheets of ray parenchyma. Unusually stimulating types of growth or traumatism recall the wide rays in regions from which they have disappeared or cause the cambium to form less complete stages of the disintegration process. These stimuli are often most effective in those regions of the plant which are supposed to be conservative, such as the first annual ring of roots and shoots, the seedling stem, and node. In the process of reduction the tissues near the entering traces of the leaves and rootlets and the peduncle are particularly retentive of primitive, unreduced characters. Stunted, suppressed, or poorly nourished cambiums hasten the reduction of wide rays by an incomplete development of specific characters. The sensitiveness of wide rays to changes in the environment or physiological activity of the plant might be anticipated when we consider the function of these sheets of parenchyma as storage organs. It is not surprising, therefore, that the effects of conservatism should have been neutralized in certain regions of the plant.

A brief description of the comparative anatomy of species which occur at various levels in this "regression" series and their behavior under different physiological conditions follows:

Fagus grandifolia.—This plant illustrates diagrammatically the structure of a species in which the multiseriate rays have suffered little or no reduction. The stem (fig. 1) possesses a ring of primary fibrovascular bundles which are separated by well developed gaps. Those arcs of the cambium which bridge these gaps, the so-called interfascicular cambiums, form ray parenchyma exclusively. As a result of their activity, multiseriate rays are formed which vary in height and width as do the gaps in the vascular cylinder. In subsequent secondary growth these "primary medullary rays," which are 2–5 cells wide, increase gradually in width and may eventually attain a breadth of approximately 15–25 cells. Next the pith these rays are in the form of long vertical lines of parenchymatous tissue. As the stem develops, these tall rays or lines of superimposed high rays are dissected into shallower rays, which are gradually deflected from their original vertical axes. The so-called fascicular cambiums form at first tracheary tissue and uniseriate rays. The latter are also high in tangential section and form long lines which are dissected in subsequent development into shorter rays. Certain of these later increase in width and may in time become as wide as the rays of the so-called interfascicular segments. With the increasing circumference of the stem, new rays are formed continually by the cambium to maintain the proper proportion of ray tissue in each radius. These shorter "secondary" medullary rays which do not extend to the pith are uniseriate at first, but may increase in width during subsequent development. In any annual layer of growth, therefore, there are rays one to many cells wide. In the first annual ring the widest rays occur in the vicinity of the nodes, on each side of traces which are about to enter the leaves.

The structure and development of rays in the ontogeny of secondary tissues in the seedling are fundamentally the same as in the mature stem. The root (fig. 2), which is commonly pentarch, possesses in cross-section five large rays that radiate from the five clusters of protoxylem. These rays are high and connect the traces of the rootlets. Although narrow when first formed, they widen rapidly and at the same time are dissected into shallower sheets of parenchymatous tissue. The other radii of the root possess at first only uniseriate rays, certain of which later increase in width as do some of the linear rays of the stem. Conditions such as have just been described occur in shoots and roots of normal development. The structure of wide rays is often different in suppressed, stunted, or feeble growth. Under these circumstances the first rays formed by the cambium are linear except in the vicinity of the traces which enter the leaves and rootlets, where multiseriate rays are persistent. In the stem the reduction of wide rays consists principally in the gradual narrowing of the sheets of parenchyma at their inner ends. In the root and the hypocotyledonary region, however, where the rays are often of considerable width, the reduction may be accompanied by slight indications of disintegration or dissection. If a shoot or root of this type receives a stimulating injury or develops suddenly a more normal type of vigor, an abrupt transition from uniseriate to wide multiseriate rays takes place, so that arcs of the cambium that have been forming linear rays and tracheary elements suddenly form only ray parenchyma (fig. 5). The phloem portion of the wide multiseriate rays, particularly in the stem, is characterized by a somewhat modified form of ray tissue. The cells of the rays become thick-walled and sclerenchymatous. At the same time the formation of ray cells upon the xylem side of the cambium is retarded, so that wedges of ray sclerenchyma project from the phloem into the xylem cylinder.

Quercus rubra.—The peduncle and the well nourished seedling stem or vigorous yearling twig of red oak resemble the normal twig of *Fagus grandifolia*, since the gaps which separate the numerous distinct clusters of protoxylem subtend an equal number of multiseriate rays. There is this difference, however, that in subsequent growth of the twigs not all of these rays increase in breadth, as do those of the vigorous seedling stem and peduncle. The multiseriate rays which occur in the first annual layer of growth of the narrow depressed segments (fig. 9) gradually decrease in width during the next two years' growth and become uniseriate. That these rays are vestiges of wide rays which have been reduced by the arrested development of the depressed segments is indicated by the fact that when the cambium loses its specialized lobed form and releases these segments, one or more of the rays may eventually increase in width from uniseriate to multiseriate. In addition, it is interesting to note that a stimulating type of injury causes these reduced rays to resume their multiseriate form.

The "secondary" multiseriate rays which are formed as the stem increases in circumference are wider and arise more abruptly than do those of the beech. These rays may be formed by the rapid widening of a simple uniseriate ray or may show indications of incipient retardation of development and be disintegrated slightly at their inner ends.

The reduction of multiseriate rays is conspicuous in feeble, poorly nourished seedlings or in stunted or suppressed twigs (figs. 4 and 10). Under such conditions of reduced vitality the first formed portions of the seedling plant may possess only uniseriate rays, although the outlines of the suppressed wide rays are clearly marked; for each gap between the primary vascular bundles subtends an aggregation of uniseriate rays or a band of tissue that is entirely devoid of vessels. These "trails," or so-called "false" rays, radiate outward and in turn subtend the multiseriate rays which are eventually formed during subsequent growth. The retarded development of "secondary" multiseriate rays is likewise marked by a trail of aggregated small rays and tissue devoid of tracheae. If the cambium of a feeble seedling receives a stimulating injury or suddenly increases in vigor, multiseriate rays are recalled at once and appear abruptly in those radii from which they have been lost.

The retardation of the development of wide rays in stunted or suppressed twigs is also marked by short trails of disintegrated ray parenchyma and tissue devoid of vessels. This process of reduction is least conspicuous, however, in the vicinity of the entering traces and in the five pairs of wide rays which separate the depressed segments from the wider wedge-shaped ones. It is not uncommon, therefore, to find in the cross-section of a young twig that during their first activity the so-called interfascicular arcs of the cambium have formed multiseriate rays in certain radii of the stem and disintegrated sheets of ray parenchyma or tissue devoid of vessels in others. As in the case of poorly nourished seedlings, stimulating types of injuries or increased vigor recall the multiseriate rays in those radii of the stem in which they have suffered suppression or disintegration.

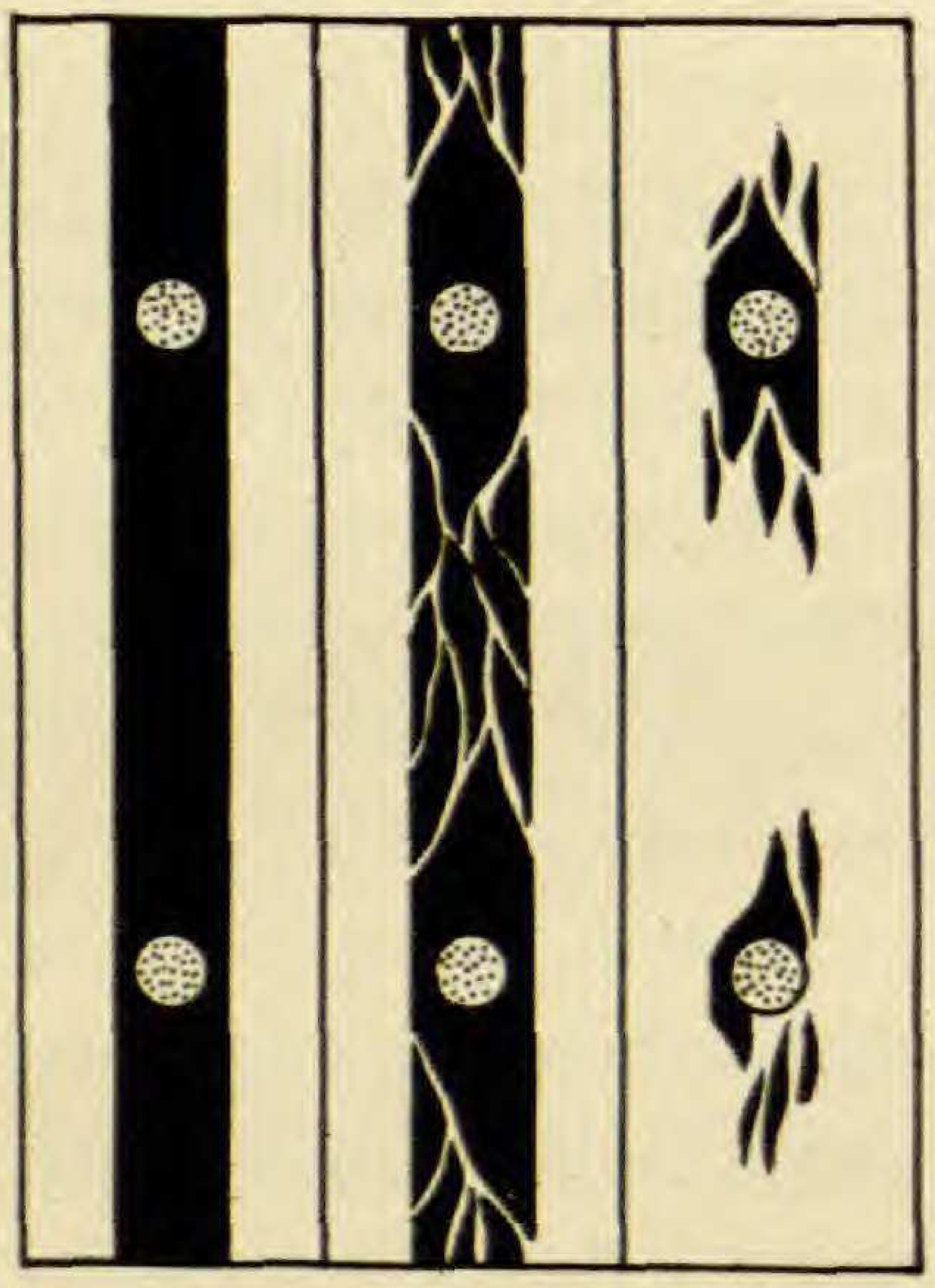

FIG. 1.—*A*, tangential section of a young root of *Fagus*, showing the vascular elements of two rootlets connected by a multiseriate ray; *B*, *Quercus* (subgenus *Erythrobalanus*), showing incipient stages of the disintegration of a wide multiseriate ray; *C*, *Quercus* (subgenus *Lepidobalanus*), showing vestiges of a multiseriate ray persisting about the vascular elements of the rootlets.

In vigorous young roots, wide multiseriate rays radiate outward from the clusters of protoxylem. These rays, as in *Fagus grandifolia*, form long vertical sheets of parenchyma which connect the traces of the outgoing rootlets (text fig. 1). Although these "primary" rays do not show well marked signs of incipient reduction, the broad alternating "secondary" multiseriate rays are in most cases considerably disintegrated at their inner ends. In less vigorous roots the primary multiseriate rays may also show evidences of reduction. However, the disintegration of these rays is most strongly shown usually at some distance from the strands of vascular tissue which supply the rootlets. Stimulating injuries or increased vitality recall the wide rays in regions of the root where their development has been retarded.

Quercus alba.—The reduction of wide multiseriate rays has progressed much farther in this oak of the subgenus *Lepidobalanus* than it has in most species of the subgenus *Erythrobalanus,* for even in vigorous, well nourished shoots and roots vestiges of wide rays persist, in the first formed secondary xylem, only in the vicinity of traces of the leaves and rootlets (fig. 6). The withdrawal of multiseriate rays from the mature shoots is accompanied by slight evidences of disintegration, but in the cotyledonary region and particularly in the root the very wide multiseriate rays are subtended by longer trails of disintegrating ray parenchyma and tissue devoid of vessels. With decreasing vigor, the multiseriate

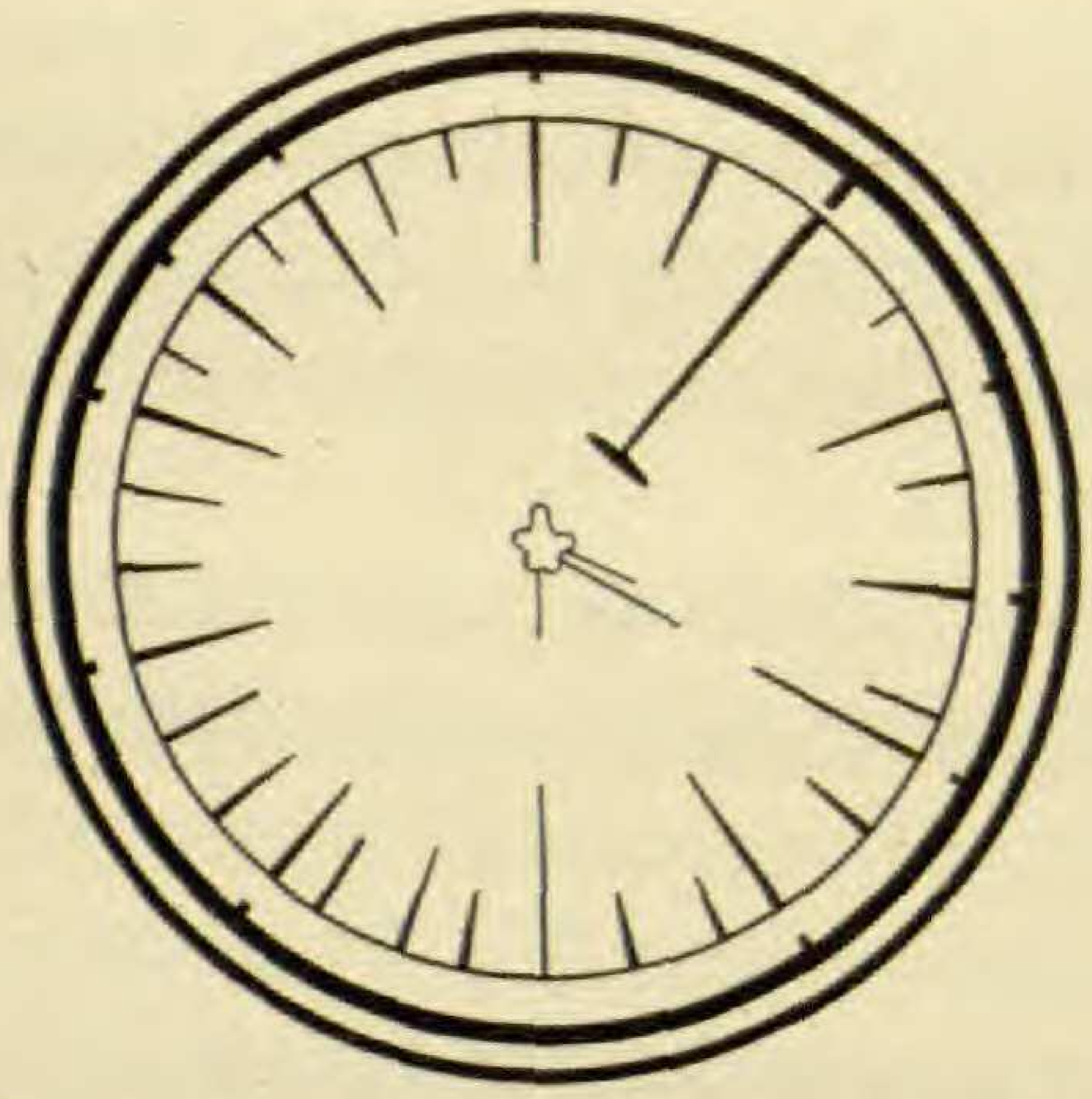

FIG 2.—Transverse section of a suppressed, forty-year-old branch of a mature specimen of *Quercus alba*, showing the retarded development of wide rays.

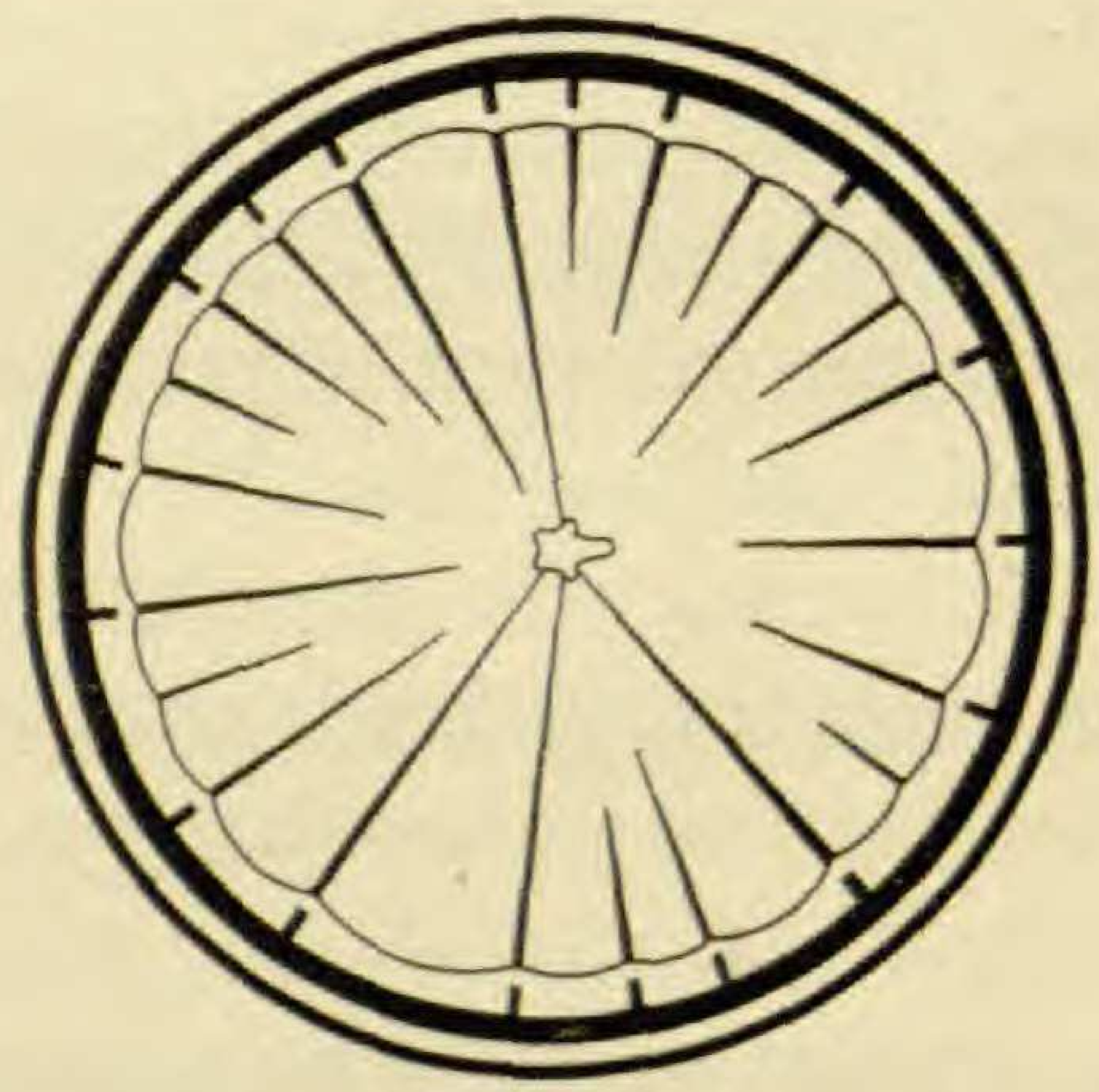

FIG. 3.—Transverse section of a vigorous, eleven-year-old shoot taken from the same tree as the suppressed branch illustrated in fig. 2.

rays appear at progressively later stages in the development of the stem and root (text figs. 2 and 3), but may be recalled by stimulating injuries or improved growth conditions.

Quercus virginiana.—In this evergreen or live oak the reduction of multiseriate rays has been carried farther than in either of the preceding species. The wide rays are commonly absent in young stems, but may be well developed in the vicinity of the vascular elements which pass out to the rootlets (fig. 17). When the wide rays appear during subsequent growth, they are much disintegrated and may persist in this dissected condition for many years, although in some cases they may finally become homogeneous ray parenchyma. This tendency for large multiseriate rays to become disintegrated not merely at their inner ends but throughout their ontogenetic development is characteristic of many tropical or subtropical species of *Quercus*. Severe, stunting types of injuries hasten the disintegration of the sheets of ray tissue, whereas stimulating or irritating injuries cause reversions to wide multiseriate rays.

Castanea dentata.—The common sweet chestnut illustrates a case in which the reduction of multiseriate rays is nearly complete. Vestiges of wide, multiseriate rays occur, however, in the first formed tissue of very vigorous roots (figs. 11 and 20) and shoots in the vicinity of the traces which pass out to the leaves and rootlets. Multiseriate rays may also be recalled by stimulating types of injuries such as are produced by the irritating effects of infections of *Endothia parasitica* (fig. 16). It is interesting to note that not only is the oak type of ray recalled but also the oak type of fiber-tracheid and leaf (fig. 18).

Betulaceae.—In the Betulaceae the reduction and disintegration of wide rays is far advanced. Typical wide multiseriate rays occur, however, somewhat sporadically in the stems of *Alnus rhombifolia* Nutt. and *A. maritima*, or may be recalled by stimulating injuries or vigorous growth in regions which do not normally possess them. In most species the rays have become entirely disintegrated except in the peduncle, where narrow multiseriate rays may be persistent. As the process of reduction is continued, these sheets of dissected ray parenchyma are replaced gradually by aggregations of multiseriate rays, and finally by bands of tissue that are merely devoid of vessels. These trails or vestiges of former multiseriate rays, so-called false rays, are frequently persistent in the vicinity of the traces of the leaves (fig. 12) and rootlets, and may remain in these regions, particularly in the first annual ring of vigorous roots and shoots, after they have disappeared from the rest of the plant. This process of reduction is accelerated by stunted, suppressed growth and retarded by vigor. The less complete stages of reduction and disintegration are recalled by stimulating injuries and unusually vigorous growth.

We have seen above that the wide multiseriate rays of the Fagales are characterized by a peculiar sclerenchymatous modification of their phloem extensions (figs. 1, 2, 7, etc.). It is significant, therefore, that these typical intruding wedges of sclerenchyma occur in the Betulaceae opposite each "false" ray of the xylem cylinder (fig. 12).

Casuarinaceae.—Successive stages of the reduction and disintegration of wide multiseriate rays, such as are found in the genus *Quercus*, occur in the shea-oaks or Casuarinas. There are several species in this family, however, in which the wide multiseriate rays are persistent in the first formed portions of the stem. In the subsequent development of these wide rays reduction and disintegration occur. These dissected sheets of smaller ray tissue become diffused through certain radii of the stem, and in this way wide multiseriate rays are replaced by narrower biseriate or triseriate ones. At the same time, certain of the uniseriate rays which occur between the wide rays widen until they become as broad as the narrow sheets of tissue which are dissected from the original wide ray. A somewhat similar phenomenon appears to have occurred in the genus *Betula*, in which narrow biseriate or triseriate rays have replaced the original wide multiseriate rays. As in the Fagales, wide multiseriate rays may be recalled in the Casuarinaceae by stimulating growth or injuries, and tend to be persistent in the peduncle and the vicinity of the traces of the leaves and rootlets.

Origin, distribution, and antiquity of multiseriate rays

Multiseriate rays of varying width are well developed in the majority of arborescent or shrubby dicotyledons and may be traced through the Tertiary to the Middle Cretaceous. These sheets of parenchyma characterize the great tropical families of woody dicotyledons, as well as those which live in a more temperate habitat. Very wide multiseriate rays occur in presumably specialized types, such as lianas, mangroves, desert plants, semi-herbaceous shrubs, etc., which are adapted to peculiar environments. The investigation of the structure and development of rays in the various families of the dicotyledons reveals much evidence that the multiseriate rays originated by the gradual widening of primitive uniseriate rays. Detailed evidence in favor of this view will be given by the writers in a subsequent paper.

Summary and conclusions

The "aggregate" ray hypothesis developed by JEFFREY and amplified by a number of students working under his direction has an important bearing upon the phylogeny of the angiosperms, since it indicates that certain of the Amentiferae are in all probability the most primitive living representatives of the phylum. There appear to be serious objections to this hypothesis, however.

OBJECTIONS TO THE "AGGREGATE" RAY HYPOTHESIS

1. The phenomenon of chalazogamy, which was considered at first of great phylogenetic value, cannot, in view of later investigations, be considered a reliable criterion for determining the phylogenetic position of plants.

2. The occurrence of so-called "aggregate" rays in the Tertiary does not appear to be significant, since "multiseriate" rays, which are considered to be a comparatively recent adaptation to the advent of a severe winter season and the consequent acquirement of the deciduous habit, are found in middle and upper cretaceous dicotyledons.

3. If "aggregate" and "compound" rays originated for the purpose of storing the assimilates descending from the persistent leaves of angiosperms in the warmer times of the Mesozoic and were later replaced by "multiseriate" rays as an adaptation to a period of refrigeration, we should hardly expect to find multiseriate rays well developed in families which have lived in tropical environments since ancient times.

4. The "aggregate" ray, which is comparatively infrequent, characterizes the obviously reduced xerophytic Casuarinaceae, and the temperate families Betulaceae, Fagaceae, and Ericaceae.

5. The "aggregate" ray hypothesis does not account for the development of "secondary" multiseriate rays nor for the origin of wide rays in the root.

6. The seedling evidence which has been advanced in favor of the origin of wide rays from congeries of uniseriate rays is invalidated by the occurrence of wide multiseriate rays in seedlings of oaks, and also in such supposedly conservative regions in this genus as the node, root, reproductive axis, and first annual ring.

"AGGREGATE" RAYS STAGES IN THE REDUCTION AND DISINTEGRATION OF WIDE MULTISERIATE RAYS

In the Fagales and Casuarinaceae there is a very complete series of form in which the progressive reduction and disintegration of wide multiseriate rays can be traced in detail. During this process of reduction the wide rays appear usually at later and later stages in ontogeny, until they finally disappear. The so-called "aggregate" rays are stages in the disintegration of wide multiseriate rays. Stimulating types of growth and injury recall the wide rays in regions where they have been lost, and are frequently most effective in those regions which are supposed to be conservative, such as the first annual ring, root, node, and seedling. Stunted, suppressed, poorly nourished types of growth, and severe distorting injuries hasten the reduction and disintegration of the wide multiseriate rays. In this process of reduction vestiges of the wide rays tend to be more persistent in the peduncle, root, and nodal regions.

THE MULTISERIATE RAY A WIDENED UNISERIATE RAY

The multiseriate ray does not appear to be of recent origin, since it is well developed in most tropical and temperate families and extends through the Tertiary at least to the Middle Cretaceous. This type of ray structure originated in all probability by the gradual increase in width of the primitive uniseriate ray.

PHYLOGENY OF THE AMENTIFERAE

One character, of course, cannot be considered conclusive evidence for assuming that a plant or group of plants is "regressive" or reduced, since all characters will not be similarly affected by changes in the environment or physiological activity, but the reduction of wide rays in the Fagales indicates that this order, as well as the Casuarinaceae, has been subjected to a strong modifying influence. This fact, taken together with the occurrence of syncarpy, epigyny, abortive ovules, and vestiges of bisexual flowers and floral envelopes, emphasizes the importance of the frequently repeated suggestion that the Amentiferae, instead of being the most primitive of angiosperms, are a group of specialized families which have reached their present more or less simple structure through reduction from earlier and usually more complicated forms.

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EXPLANATION OF PLATES III–V

FIG. 1.—Transverse section of a seedling stem of *Fagus*, illustrating the structure, development, and distribution of multiseriate rays which have not suffered reduction.

FIG. 2.—The same; young root.

FIG. 3.—Transverse section of a vigorous young seedling stem of *Quercus rubra*, showing multiseriate rays which radiate from each wide gap in the primary elements.

FIG. 4.—The same; less vigorous seedling stem, showing the disintegration and reduction of wide rays and their recurrence in tissue which has been formed under the stimulating effects of an injury.

FIG. 5.—Transverse section of a suppressed seedling of *Fagus*, showing the arrested development of wide multiseriate rays in the first formed portion of the hypocotyledonary stem and their sudden recurrence after a stimulating type of injury.

FIG. 6.—Transverse section of a young root of *Quercus* (subgenus *Lepidobalanus*), showing the reduction of multiseriate rays; "trails" of aggregated uniseriate rays mark the former position of the wide rays; in one radius vestiges of a multiseriate ray have persisted in the vicinity of the outgoing vascular elements of a rootlet; in another portion of the root a stimulating type of injury has recalled wide homogeneous sheets of ray parenchyma.

FIG. 7.—Transverse section of the seedling stem of *Casuarina suberosa*, showing the disintegration and reduction of wide rays.

FIG. 8.—Transverse section of a peduncle of the same species, showing well developed multiseriate rays.

FIG 9.—Transverse section of a vigorous young shoot of *Quercus* (subgenus *Erythrobalanus*), showing five depressed segments and multiseriate rays.

FIG. 10.—Transverse section of a stunted, slow growing branch of *Quercus* (subgenus *Erythrobalanus*), showing the reduction of multiseriate rays, their persistence on either side of the depressed segments, and their recurrence in tissue stimulated by injuries.

FIG. 11.—Transverse section of a very vigorous young root of *Castanea dentata*, showing the persistence of vestiges of wide rays in the vicinity of the vascular elements which supply the rootlets.

FIG. 12.—Transverse section of a shoot of *Alnus*, showing the persistence of "trails" of uniseriate rays about the lateral leaf-traces and their recurrence in traumatic tissue.

FIG. 13.—Transverse section of a portion of a vigorous seedling stem of *Quercus rubra;* two multiseriate rays radiate from the gaps between three clusters of primary elements; $\times 45$.

FIG. 14.—Transverse section of a portion of a less vigorous seedling stem of *Quercus rubra*, showing the reduction and disintegration of two multiseriate rays; $\times 45$.

FIG. 15.—Transverse section of part of a two-year-old peduncle of *Quercus coccinea*, showing multiseriate rays; $\times 80$.

FIG. 16.—Transverse section of traumatic tissue of *Castanea dentata*, showing oaklike multiseriate rays and fibers recalled by the stimulating effects of *Endothia parasitica;* $\times 130$.

FIG. 17.—Transverse section of a portion of the hypocotyledonary stem of *Quercus virginiana*, showing wide multiseriate ray subtended by protoxylem; $\times 20$.

FIG. 18.—Reversionary leaf of *Castanea dentata*, showing oaklike characters recalled by the stimulating effects of *Endothia parasitica;* $\times \frac{1}{2}$.

FIG. 19.—Transverse section of the first formed portion of a depressed segment of a vigorous shoot of *Quercus velutina;* multiseriate rays radiate from each gap in the primary vascular cylinder; $\times 45$.

FIG. 20.—Transverse section of the first formed portion of a very vigorous root of *Castanea dentata*, showing vestiges of multiseriate rays; $\times 15$.

FIG. 21.—Transverse section of the primary root of *Quercus alba*, showing the recurrence of multiseriate rays under the stimulating effects of an injury; $\times 5$.